

## REVISION OF THE MULTIPHASED GENUS CORBULIPORA MACGILLIVRAY (BRYOZOA: CRIBRIMORPHA)

P.E. BOCK<sup>1</sup> AND P.L. COOK<sup>2</sup>

<sup>1</sup>School of Ecology and Environment, Deakin University, 661 Blackburn Road, Clayton, Vic. 3168, Australia  
(pbock@deakin.edu.au)

<sup>2</sup>Honorary Associate, Museum Victoria, GPO Box 666E, Melbourne, Vic. 3001, Australia

### Abstract

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*Corbulipora* MacGillivray is redefined to include only species which occur in successive growth phases. The fossil type species, *Corbulipora ornata* MacGillivray, occurs in an encrusting ancestrulate phase, an erect quadriserial, ovicellate phase, and a frontally-budded partially kenozooidal phase. The encrusting ancestrulate phase of the Recent species, *C. tubulifera* (Hincks), is the type species of the genus *Acanthocella* Canu and Bassler, which is a junior synonym of *Corbulipora*. The succeeding, ovicellate, flustrine phase, known as *Watersia militaris* (Waters), is the type species of *Watersia*, another junior synonym of *Corbulipora*. It produces a third bilaminar phase known as *C. oriparma*, a synonym of *C. tubulifera*. This has rhizoids and develops further flustrine phases. Fossil specimens assigned to *Acanthocella tubulifera* in the past are here considered to be the primary encrusting phase of a bilaminar phase, known as *Corbulipora suggestens* (Waters), from which it has become separated. A thinly calcified intervening erect phase similar to the flustrine phase of *C. tubulifera* is inferred to have existed but not to have been preserved as a fossil. Some species previously referred to *Watersia* are assigned to *Klugeflustra* Moyano which, like *Neoflustra* Lopez Gappa, has flustrine colonies with large, hyperstomial ovicells, unlike those of the family Flustridae sensu stricto. A key to species of *Corbulipora* and their various phases is given.

### Introduction

The superfamily Cribrilinoidea Hincks, as redefined and interpreted by Gordon (1984: 60), includes not only all the genera usually assigned to the family Cribrilinidae Hincks (for example, Bassler, 1953: G184), but all those referred to the Cribrimorpha by Lang (1916). Many of the Cretaceous genera described by Lang were included in the family Pelmatoporidae by Larwood (1962: 51). Voigt (1993) also assigned Cretaceous species to this family.

'Cribrimorphs' are characterized by the presence of a frontal shield of hollow calcified spines which overarch a membranous frontal wall with contiguous, uneocalcified primary orifice and operculum. Obviously, many 'anacean' genera share these characteristics and the resulting shifts in systematic position of various species of *Calloporella* and *Membraniporella* (Ryland and Hayward, 1977), emphasise Levinsen's (1909: 156) opinion of the 'unnaturalness' of the family Cribrilinidae. Gordon (1984: 60–61) noted the similarities among some species of Calloporidae with those of *Membraniporella* and *Figularia* and

remarked 'at present it is difficult to define positively the boundaries between the two families.' Moyano (1984, 1991) suggested some preliminary groupings of cribrimorphs based on frontal shield structures. These include some with umbonulomorph affinities but do not deal with some intermediate forms. It remains difficult to define any polythetic boundaries among superfamily and family groups, which are themselves almost certainly non-homogeneous.

However difficult it may be to define cribrimorphs exclusively, many species with distinctive characteristics have been described. Detailed examination of some apparently ubiquitous taxa has recently yielded much more information on ovicell ontogeny and on kinds and degrees of polymorphs, which have revealed many exclusive groups of character correlations, and have greatly increased the number of described species (Ristedt, 1985; Bishop and Househam, 1987; Harmelin and Aristegui, 1988).

Briefly, the frontal shield (pericyst) is formed by spinous outgrowths (costae) which are hollow outfoldings of the calcifying marginal frontal

wall (gymnocyst). The costae extend over the flexible part of the frontal wall (frontal membrane) and fuse centrally (median area of fusion, Larwood, 1962). The central coelomic space of each eosta is in contact, at its origin, with the perigastric (or visceral) coelom of the zooid (Wass, 1975). Small uncalcified areas regularly spaced along the lateral vertical faces of each eosta have the potential to expand their overlying cuticle intussusceptively and to calcify and form fusions with those of neighbouring eostae leaving holes between successive eostae (lacunae). Other small unealcified areas, equally regularly distributed along the upper (frontal) surface of each eosta (lumen pores or pelmatidia), allow similar expansions of cuticle and underlying coelom frontally. These may also calcify forming spinous processes. Sometimes the most marginal pelmatidia, which are usually the largest, extend as spinous processes which meet those of neighbouring zooids, forming interzooidal fusions quite late in ontogeny. This may produce secondary calcification and even tertiary interzooidal shields or extrazooidal expanses (Wass, 1975). In some species frontally budded zooids arise from expansions originating from enlarged pelmatidia, which then function very like the frontal septular pores of many ascophorans allowing transfer of coelom and nutrients to the developing buds.

Interzooidal communication through both septular pores, pore-chambers and a special kind of pore-chamber (here called a chambered pore) all occur in species of *Corbulipora*. The chambered pores allow another form of frontal budding. They originate as a fairly simple uniporous or multi-porous pore-plate at the base of a vertical wall. This rapidly develops a large calcified chamber with a window covered by cuticle on the upper and outer side. These chambers may encompass more than one septular pore. Some zooids of the same astogenetic generation may communicate directly through septular pores, others through septular pores on both sides of a chambered pore. This often expands frontally between the vertical zooid walls, forming a kenozooid with an unealcified window at its frontal side. These kenozooids tend to occur at the 'corners' between autozooids and are very evident at the growing edges of colonies; they are also the origin of rhizoids and 'stalk' kenozooids. Somewhat similar kinds of pore-chambers have been described in the family Hippothoidae by Gordon and Hastings (1979) but these are much more regular in size, shape and distribution than

the chambered pores. It is interesting, however, that Gordon (1989) noted that an ability to produce frontal buds from the windows of such pore-chambers was a definitive character of his Infraorder Hippothoomorpha and he considered that there was a 'kind of conceptual linkage, from the Cribriolinaidea through Catenicelloidea to Hippothooidea'.

The potential for considerable astogenetic and ontogenetic change within a colony is thus present in cribrimorph morphology. Although almost every possible resultant structure seems to be produced in *Corbulipora*, in general, this potential does not seem to be realized among other cribrimorph genera. Pelmatidia are not always present, or are little-developed, and interzooidal frontal buds are rare. Species may thus be defined by such characters as the proportion of the gymnocyst to the pericyst, the number and form of costae, and the extent and nature of the median area of fusion. Patterns of kenozooids and ovicells, together with avicularia, also seem to define many taxa in detail and to have character consistency (Ristedt, 1985; Bishop and Househam, 1987). The species of *Corbulipora* described below pose problems precisely because they display a wide range of ontogenetic changes, coupled with the occurrence of multiple astogenetic phases in which the contributing zooids are often completely unlike one another; in one case being totally 'un-cribrimorph' in appearance (Bock and Cook, 1994).

Colonies in which the zooids exhibit zones or areas of totally differing morphologies are not unknown in other Bryozoa. Frequently isolated zones or areas have been assigned to completely unrelated taxa and Voigt (1975) has illustrated several examples drawn principally from the Late Cretaceous of Northern Europe. Among these, one cribrimorph, *Castanopora bipunctata* (Goldfuss), shows remarkable autozooidal heteromorphy. Colonies are bilaminar, unilaminar, or occasionally encrusting. In all these colony forms, entire fragments or large areas within colonies have membraniporine zooids with no trace of a calcified eostal shield frontally. In other specimens, all or most of the zooids have a shield composed of 10–18 eostae with pelmatidia, which alternate with rows of small lacunae. Both types of autozooid bear identical ovicells, and like some phases of *Corbulipora tubulifera*, identical kinds of large avicularia occur in both kinds of colony. *Castanopora bipunctata* does not, however, seem to occur in isolated subcolonies, each repre-

senting a distinct phase, and thus differs from *Corbulipora*.

Specimens from the collection of Dr Shizuo Mawatari, and from the following institutions have been examined: Australian Museum, Sydney (AM), Natural History Museum, London (BMNH), Museum of Victoria, Melbourne (NMV) and the Zoological Museum, Copenhagen (ZMC).

#### *Corbulipora* MacGillivray

*Corbulipora* MacGillivray, 1895: 60.—Wass 1975: 168.

*Watersia* Levinson, 1909: 94.

*Acanthocella* Canu and Bassler, 1917: 35.

Type species. *Corbulipora ornata* MacGillivray, 1895.

**Description.** Complete colonies consisting of subcolonies with encrusting, erect and/or semi-erect phases of growth. Each phase with zooids of consistent morphologies, which may differ completely from those of a preceding or succeeding phase. Each species including at least 1 cribrimorph phase, usually more. Growth sequences always beginning with an encrusting ancestrula phase but other sequences may alternate or co-exist, although sometimes in physical isolation. All phases are known, or assumed, to be capable of a separate existence. Ancestrula tati-form, with marginal spines. Zooids of all cribrimorph phases with gymnocyst and pericyst of costae with pelmatidia and lacunae. Oral spines 1–3. Ovicells often confined to 1 phase only but not necessarily the same phase in different species. Ovicells are prominent, hyperstomial, closed by operculum, with median suture and paired entoocial frontal areas. Brooding zooids of flustrine phase with flattened spines or with exposed frontal membrane and enlarged oral spines only. Avicularia interzooidal, large, with distally orientated rostrum, rounded or expanded terminally.

**Remarks.** Multiphased growth is known or may be reliably inferred to occur in each of the three species here referred to *Corbulipora*. In *C. ornata*, all zooids of the three phases recognized have costate pericysts. The first phase is encrusting, the second erect and quadriserial, and this phase develops both avicularia and ovicells. The third phase is frontally budded from the pelmatidia of the second erect phase zooids and is often purely kenozooidal. In *C. suggerens*, two

cribrimorph phases have been recognized and inferred to belong to one taxon. One phase is encrusting, the other is bilaminar. Its colony and zooid morphologies are so akin to those of the third, bilaminar phase of *C. tubulifera*, that it seems almost certain that it represents a third phase, and that a missing, intervening, erect second phase, with very thin calcification, and perhaps flustrine or cellularine growth, once occurred, but was not preserved in the fossil material. The bilaminar phase of *C. suggerens* occasionally bears ovicells, unlike that of *C. tubulifera*. This last species has been observed with its three phases growing from one another. The ancestrula encrusting phase gives rise to several flustrine subcolonies which alone bear ovicells. Large avicularia occur in this phase and in the third phase, which develops from the tips of the flustrine fronds. These two phases may alternate (Bock and Cook, 1994). Recently a further living species of *Corbulipora*, *C. inopinata*, has been described from southwestern Australia by Bock and Cook (1998). It closely resembles *C. tubulifera* and also occurs in three sub-colony phases. The flustrine, second phase differs in having zooids with frontal spines, somewhat resembling those of the earlier ontogenetic stages of the second, quadriserial phase of *C. ornata*.

The genus *Corbulipora* was introduced for *C. ornata* alone. Wass (1975) redefined the genus and assigned some species to a new subgenus, *Anaskopora*. These species, together with *Cribrilina cornuta* MacGillivray (1895), which Wass (1975) referred to *Corbulipora*, are now regarded as generically distinct and are discussed elsewhere (Bock and Cook, 2001).

*Corbulipora collaris* Canu and Bassler (1920: 308, pl. 43 fig. 14), from the North American Eocene was also redescribed by Wass (1975: 170, pl. 8, figs 7–9). It has medially orientated adventitious oral avicularia and an endozoooidal ovicell. It is therefore excluded here from *Corbulipora* which is considered to have a Tertiary to Recent, Australasian distribution only. When Wass (1975) revised *Corbulipora*, *C. collaris* was the only species assigned to the genus in which an ovicell had been described. This was probably the reason why he used the term ‘entozoooidal’ for the ovicell type, which he then applied to the whole genus. All ovicells now observed in species referred to *Corbulipora* are hyperstomial, with paired, entoocial frontal areas.

### Key to species and phases of *Corbulipora*

1. Subcolony flustrine, autozooids with exposed frontal membrane and 1 pair of oral spines. Ovicells and large interzooidal avicularia present ..... *C. tubulifera* phase 2
- Subcolony not flustrine, autozooids with costal frontal shield ..... 2
2. Subcolony encrusting a substratum, mostly single layered ..... 3
- Subcolony erect, subereet and bilaminar or formed by frontal budding ..... 5
3. Autozooids large ( $L_z > 0.75$  mm), costae 16–24, with 3–4 concentric series of long, sometimes branched, spinous processes arising from pelmatidia ..... *C. suggestens* phase 1
- Autozooids smaller, costae 10–18, with 1–2 concentric series of blunt tubercles arising from pelmatidia ..... 4
4. Autozooids very small ( $L_z < 0.50$  mm), orifice small (to 0.10 mm). Lateral oral spines raised, inflexed and fused above the orifice ..... *C. ornata* phase 1
- Autozooids larger ( $L_z > 0.60$  mm), orifice larger (to >0.11 mm). Oral spines not raised or fused ..... *C. tubulifera* phase 1
5. Subcolony erect, quadrilateral; autozooids with long gymnocyst and small costal shield. Avicularia rare, ovicells present ..... *C. ornata* phase 2
- Subcolony composed of autozooids and kenozooids, budded frontally from phase 2-zooids, orientation random. Gymnocyst and orifice not generally visible; avicularia and ovicells absent ..... *C. ornata* phase 3
- Subcolony bilaminar, small; autozooids orientated distally, interzooidal avicularia present ..... 6
6. Subcolony triangular, arising from 2–4 zooids with partially calcified frontal shields, orifices not occluded by oral spines. Avicularia not raised distally, with a bar. Ovicells present ..... *C. suggestens* phase 3
- Subcolony rectangular, arising from 6–8 zooids with partially calcified frontal shields, orifices often occluded by growth and fusion of oral spines. Avicularia raised distally, with paired condyles. Ovicells absent, rhizoids present ..... *C. tubulifera* phase 3

***Corbulipora ornata* MacGillivray**

Figures 1–9, 27, Tables 1, 2

*Corbulipora ornata* MacGillivray, 1895: 60, pl. 8 figs 20, 21.—Maplestone, 1904: 201 (listed).—Brown, 1958: 54.—Wass, 1975: 168, pl. 7 figs 1, 2.

**Material examined.** Lectotype (chosen by Wass, 1975); NMV P27642, Schnapper Point (= Balcombe Bay), Victoria, Middle Miocene, Balconian.

Other material. Balcombe Bay; Cooriemungle, near Princetown and Princetown, Victoria (Middle Miocene, Balconian); Bird Rock, near Torquay, Victoria (Upper Oligocene, Janjukian); Mount Schanck, S of Mount Gambier, South Australia (Lower Miocene, Longfordian).

**Distribution.** Additional localities given by MacGillivray (1895) and Maplestone (1904) include: Cape Otway, Spring Creek, Campbells Point, Mornington, Mitchell R. and Bairnsdale; localities given by Brown (1958) include: Localities XVI (Glenaulin Clay) and XXVI (Wataepoolan Limestone) near Crawford R.; and XXII and XXIII on Glenelg R., Nangela, south-

western Victoria. Miocene to Oligocene (see Appendix).

**Description.** *Corbulipora* with subcolonies of 3 growth phases: all zooids with costate pericysts. Subcolonies of encrusting phase very small, comprising at most 40 zooids; basal walls calcified only at margins. Ancestrula has 14–16 marginal spines and buds a triad of distal primary zooids. As in *C. suggestens*, appearance of some zooids differs from those budded later in astogeny. Autozooids have small, distinct gymnocyst, and pericyst with 10–16 costae, each with 2 or 3 intervening lacunae and 2 pelmatidia, raised as blunt tubercles. Secondary calcified orifice small, with paired condyles and 3 oral spines, lateral pair often raised vertically, inflexed and fused above orifice (Figs 1, 2). This condition also occurs in some zooids of third phase, which may resemble those of first phase closely. Zooids communicate through small pore-chambers at base of vertical walls.

Second phase erect and quadrilateral, zooids

Table 1. Comparative measurements in mm among phases in species of *Corbulipora*. Lz, lz, length and width of zooid; lo width of orifice.

<i>C. ornata</i>	<i>C. suggestens</i>	<i>C. tubulifera</i>
Phase 1	Phase 1	Phase 1
Lz 0.45–0.48	Lz 0.58–0.87	Lz 0.58–0.74
lz 0.37–0.40	lz 0.37–0.54	lz 0.38–0.50
lo 0.08–0.09	lo 0.11–0.13	lo 0.12–0.13
Phase 2	Phase 2	Phase 2
Lz 0.70–1.00	—	Lz 0.78–1.32
lz 0.28–0.36	—	lz 0.25–0.33
lo 0.13–0.14	—	—
Phase 3	Phase 3	Phase 3
Lz 0.33–0.37	Lz 0.58–0.87	Lz 0.54–0.87
lz 0.33–0.37	lz 0.37–0.54	lz 0.32–0.54
lo 0.07–0.10	lo 0.06–0.12	lo 0.10–0.14

Table 2. Comparative measurements in mm among phases of *Corbulipora* and species of *Klugeflustra*. Lz, lz, length of zooid; Lav, lav, length and width of avicularium; Lp, length of palate; Lov, lov, length and width of ovicell.

	Lz	lz	Lav	lav	Lp	Lov	lov
<i>C. ornata</i> phase 2	0.70–1.00	0.28–0.36	0.55–0.66	0.17–0.21	0.43–0.55	0.24–0.25	0.23–0.25
<i>C. suggestens</i> phase 3	0.58–0.87	0.37–0.54	0.28–0.43	0.12–0.16	0.12–0.20	0.12–0.16	0.16–0.21
<i>C. tubulifera</i> phase 2	0.78–1.32	0.25–0.33	0.65–0.96	0.22–0.26	0.31–0.35	0.23–0.27	0.28–0.33
<i>K. vanhoeffeni</i>	1.23–1.56	0.40–0.50	1.03–1.25	0.25–0.33	0.40–0.50	0.50–0.60	0.44–0.48
<i>K. kishakaensis</i>	1.32–1.43	0.32–0.36	0.25–0.37	0.32–0.31	0.08–0.10	0.33–0.43	0.40–0.47
<i>K. simplex</i>	0.44–0.50	0.15–0.19	—	—	—	0.21–0.28	0.28–0.31

communicating through simple septular pores. Branches bifurcate occasionally. Intermediate developmental stages linking encrusting with quadriracial phase unknown, and in isolation, component zooids of the 2 phases totally unlike. Erect-phase autozooids have elongated, smooth gynoecyst surrounding costal shield which may be subrectangular or small and oval. Zooid length nearly twice that of those from other phases, 12–22 costae, distal pair forming suboral bar, prominent and sloping forward on distal edge (Fig. 4). Secondary calcified orifice large, almost perpendicular to frontal shield, with 1 pair of small lateral spines. Costae expanded and fused terminally; variable median area of fusion which changes its aspect with ontogeny. Costae bearing 2 or 3 small pelmatidia which alternate with 2–4 laeunae. Ovicells generally rare, narrow, with paired, crescentic, entoocelial frontal areas. Oral spines of brooding zooids greatly enlarged, raised

and fused above orifice, like those of phase 1 zooids; spines also bear some pelmatidia (Fig. 27). Avicularia also rare; large, with distinct gynoecyst, in series with autozooids. Rostrum rounded or expanded terminally, and orientated distally; small paired condyles (Fig. 3).

Subcolonies of third phase arise by frontal budding directly from autozooids of second phase. Zooid buds develop from greatly expanded pelmatidia; kenozooids and autozooids produced; ovicells and avicularia absent. Frontally budded zooids have random orientations; frontal shields have 10–16 costae, each with 2 or 3 pelmatidia raised into long spinous processes. These interdigitate and sometimes fuse interzooidally, especially at margins of zooids, forming continuous secondary shield in some specimens. Secondary, calcified orifice very small, with 3 oral spines. These may be long and prominent, occasionally raised, inflexed and fused above orifice, exactly

as in encrusting zooids of first phase, not occluding orifices (compare *C. tubulifera*), but many zooids have no obvious orifice. Some may have been occluded by general interzooidal fusion of spinous processes but others seem to have been budded with no orifice, and are therefore true kenozooids.

**Remarks.** The taxonomic identity of the first and second phases of *C. ornata* can only be inferred, since zooids of intermediate morphologies have not been found linking them in situ. The ontogenetic changes in second-phase zooids leading to the third phase can, however, be traced in many specimens from Balcombe Bay and Mount Schanck. Early in ontogeny, the pericysts of the erect second-phase zooids form a small, oval area distal to an elongated gymnocyst (Fig. 3). The costae are long and virtually without lateral fusions, so that the intervening, slit-like lacunae extend to a narrow median area of fusion. Ontogenetic changes begin with a widening of this area by the development of lateral costal fusions, and a thickening of the shield by expansion of the pelmatidia and growth of spinous processes frontally (Fig. 4, 5). Some pelmatidia continue to increase in size, particularly those on the thickened suboral bar, and they become blister-like, while the more lateral spinous processes fuse interzooidally. The third-phase buds arise directly from expanded pelmatidia and some appear to develop as chambered pores or small interzooidal kenozooids (Figs 6, 7). The larger kenozooids and some autozooids have costate perieysts with numerous, long spinous processes arising from their pelmatidia. The third phase forms small, globular masses, budding from and overgrowing the second-phase zooids especially at the bifurcations of erect branches. In some specimens secondary calcification results in the third phase appearing as a globular mass of spinous or ridged costae with no orifices and no distinct zooidal structure remaining. The zooids of the second phase remain visible protruding at the proximal and distal ends of the mass (Figs 8, 9).

#### *Corbulipora suggereus* (Waters)

Figures 10–16, 28–29, Tables 1, 2

*Cribrilina suggereus* Waters 1881: 327, pl. 17 fig. 75.—MaeGillivray, 1895: 57, pl. 8 fig. 8.—Maplestone, 1904: 201 (listed).

*Cribrilina tubulifera* Waters, 1883: 436 (not Hincks, 1881).

*Acanthocella tubulifera*.—Brown, 1958: 54 (fossil specimens only).

*Cribrilina jonesi* Brown 1958: 52, fig. 28.

*Corbulipora* sp.—Wass and Yoo, 1975: 811, pl. 2 fig. 4.

*Corbulipora suggereus*.—Bock and Cook, 1994: 34, fig. 6.

**Material examined.** NMV P73147, Holotype of *C. jonesi*, locality IX, E bank of Glenelg R., Myaring, south-western Victoria (Middle Miocene, Balcombian).

Other material, Balcombe Bay (ovicells); Coorie-mungle; Prineetown (ovicells); Grieves Creek; Bairnsdale (all Middle Miocene, Balcombian); Narrawaturk Bore 2, near Peterborough, Victoria and Mount Schanck, South Australia (both Lower Miocene, Longfordian).

**Distribution.** Additional localities given by MacGillivray (1895) and Maplestone (1904) include: Campbells Point, Curdies Creek, Muddy Creek, Mitchell R. and Schnapper Point; and by Brown (1958) include Locality XIV, section at West end of Caldwell's Cliff, Glenelg R. (Miocene, Myaring beds) (see Appendix).

**Description.** *Corbulipora* with subcolonies of 2 known growth phases. Ancestrula tafiform, with 10–12 marginal spines. Autozooids of first, encrusting phase large, oval, with distinct rim of smooth gymnocyst surrounding costal shield with 16–24 costae (Fig. 10). Secondary, calcified orifice smaller than that of *C. tubulifera* (compare figs 16, 17), with 3 oral spines and paired condyles. Costae with 3, occasionally 4 pelmatidia and 3 or 4 lacunae. Median area of fusion increases in width with astogeny, and pelmatidia become raised and tuberculate, with long, sometimes branched spinous processes, which interdigitate and occasionally fuse laterally. Zooids with typical pore-chambers, with 3 distal and 1 or 2 lateral windows within gymnocyst boundary (Fig. 10). Avicularia and ovicells absent.

Bilaminar phase forming small, subtriangular subcolonies, each arising from 2–4 zooids which have frontal shields uncalcified or calcified only at distal end (Fig. 12). Subcolonies expand by bifurcation of zooid rows to 4–6 within two astogenetic generations. Basal lamina between the 2 zooid faces with few septular pores; autozooids with 2 or 3 large chambered pores or kenozooids laterally and distally (Figs 13–15). Autozooids of first 2 generations of completely calcified zooids often have elongated costal shields with little or no gymnocyst visible, and 16–22 costae. Distal pair of costae form prominent suboral bar sloping forward on distal edge, obscuring large, wide, vertical secondary calcified orifice. Costae well-separated marginally with 2 or 3 intervening lacunae and 3 concentric rows of tuberculate pelmatidia. Autozooids of next 2 or 3 generations with increasingly short, rounded costal shields,

with some marginal gymnocyst visible; 10–16 eostae, distal pair forming suboral bar defining a minute, semicircular orifice, with paired condyles and 3 oral spines, which is visible frontally (Fig. 16). Pelmatidia arranged in 3 raised concentric series, with spinous processes which may interdigitate and fuse laterally. Oral spines often long but do not fuse above or occlude orifice. At growing margin of subcolonies, large, blister-like chambered pores or kenozooids occur in adjacent series between autozooids (Figs 13–15). Avicularia only among zooids of proximal, earlier astogenetic generations of subcolonies; large and interzooidal, with distally orientated, subspatulate rostrum and complete bar (Fig. 12). Ovicells rare, only on those zooids on proximal margin of phase 3 subcolonies, where zooids lack any calcified, costal frontal shield. Ovicells slightly flattened frontally, with paired entoocelial areas, which in a few cases show signs of eostate structure (Figs 28, 29). Unlike brooding zooids of *C. ornata* and *C. tubulifera*, paired oral spines not enlarged.

**Remarks.** The encrusting and bilaminar phases of *C. suggerens* resemble the equivalent first and third phases of *C. tubulifera* closely. The encrusting zooids are usually larger and in early astogeny exhibit a dramatic change in appearance between the generations like those of *C. ornata* at the same astogenetic stage. The vertical, marginal parts of the eostae are well separated and the median area of fusion is narrow. There are only two concentric series of pelmatidia with short, but distinct spinous processes. In the next generations, zooids have wider median areas of fusion and three or more series of spinous processes. In some specimens from Princetown, a large distal pore-chamber forms an irregular distal kenozooid with a single pore in its frontal surface. The pore-chambers do not normally protrude beyond the base of the gymnocyst, unlike those of *C. tubulifera*. The zooids of the bilaminar phases of the two species resemble one another closely, but the size and shape of the subcolonies differ. The narrow origin of those of *C. suggerens* suggest that they may have been derived from the tips of a quadrilateral, or very narrow, thinly calcified phase which has not been preserved. This in contrast to the much wider colonies of *C. tubulifera*, which are known to be derived from the broader, flustrine, *Watersia*-phase fronds. The orifices of the zooids of *C. suggerens* are not occluded by oral spine development, and the avicularia also differ from those of *C. tubulifera* in having a flat rostrum and a complete bar. Finally, as mentioned

above, the bilaminar phase of *C. suggerens* occasionally bears ovicells proximally, unlike that of *C. tubulifera*.

Waters's (1883) record of *C. tubulifera* from Muddy Creek seems to have been based on specimens of the encrusting phase of *C. suggerens*, which he described as growing on shell (see above). He noted that the autozooids had larger orifices than those of his specimens of bilaminar *C. suggerens* where they are extremely small. Brown (1958) introduced *Cribriolina jonesi* for another bilaminar species from the Victorian Tertiary. The zooids had 16 eostae and a thick suboral bar, and he noted their resemblance to *Acanthocella tubulifera*, which he regarded as a senior synonym of *C. suggerens*. Brown remarked on the small size of the orifice. The holotype of *C. jonesi* has been examined and proves to be identical with the bilaminar phase of *C. suggerens*.

#### *Corbulipora tubulifera* (Hincks)

Figures 17–26, 30–32, Tables 1, 2

*Cribriolina tubulifera* Hincks 1881: 8, pl. 1 fig. 7.—Waters, 1887b: 187, pl. 5 figs 2, 6.

*Acanthocella tubulifera*.—Brown, 1958: 52 (lectotype only, see *C. suggerens*).

*Flustra militaris* Waters 1887a: 93, pl. 14 fig. 2.

*Watersia militaris*.—Levinsen, 1909: 94, 95 (not Livingstone, 1929; 53; not Gordon, 1986: 28).

*Corbulipora* sp.—Wass, 1973: 361, pl. 1 figs 1–4.

*Corbulipora oriparma* Wass 1975: 169, pl. 9 figs 1–7, pl. 10 figs 1–6, 9–11.—Cook, 1979: 271, fig. 1D.—Wass and Yoo, 1983: 323.

*Corbulipora tubulifera*.—Bock and Cook, 1994: 33, figs 1–5.

**Material Examined.** BMNH 1899.5.1.726, photograph of lectotype of *C. tubulifera*, Bass Strait, BMNH 1887.10.21.1, ?part of type material of *W. militaris*, Port Jackson, Waters coll. BMNH 1926.6.1.2, Port Jackson, 9–15 m, label in Waters's hand 'sandy mud bottom near the Heads'. BMNH 1897.5.1.447, Port Jackson. AM U5006, 'Endeavour' Exped., T.Mortensen, S of Lakes Entrance, Victoria, 38°15'–25'S, 148°20'–43'E, 128–220 m, 8–9 Sep 1914, sand. NMV Bass Strait Survey: Kimbla stn 99 40°06'S, 143°16'E, 11 Oct 1980, 139 m; stn 100, as above, 158 m; stn 101, as above, 187 m. Sarda stn 112, 40°22'S, 145°127'E, 3 Nov 1981, 40 m. Hai Kung stn 135, 40°50'S, 146°31.3'E, 4 Feb 1981, 68 m. Tangaroa stn 155, 38°34'S, 144°54.3'E, 12 Nov 1981, 70 m; as above, 75 m; stn 164, 40°40.7'S, 148°36.9'E, 14 Nov 1981, 67 m. SLOPE stn 22, 37°0.6'S, 150°20'E 21 Jul 1986, 363 m; stn 45, 42°2.2'S, 148°38.7'E, 27 Jul 1986, 800 m; stn 46, as above, 720 m; stn 47, 41°59'S, 148°38.8'E, 27 Jul 1986, 500 m. ZMC, Port Jackson, NSW (label in Waters's hand).

**Description.** *Corbulipora* with subcolonies of 3 growth phases, 2 of which may be sequential as well as alternating. Observed sequences include encrusting (phase 1) to flustrine (phase 2); flustrine to bilaminar (phase 3); and bilaminar to flustrine (Fig. 18).

Phase 1. Subcolony encrusting small fragments of shell, dead bryozoans etc. Ancestrula tiform with 10–14 fine marginal spines (La 0.45 mm) (Figs 23). Subcolony forming small patch of 50–100 zooids, basal walls calcified only marginally. Autozooids with marginal gymnocyst and pericyst of 10–16 stout costae. Vertical marginal part of costae well separated, inflexed and abutting centrally to form wide median area of fusion, alternating with short rows of 2 or 3 lacunae. Pelmatidia in 2 concentric circles, raised, forming blunt tubereles, occasionally spinous. Suboral bar swollen, with 3 or 4 pelmatidia. Secondary, calcified orifice semieircular with pair of small condyles and 3 oral spines. Operculum golden brown, closely apposed to the calcified orifice. 1 distal and 2 or 3 large lateral chambered pores, each enclosing several small septular pores. Each marginal chamber capable of giving rise to 1 rhizoid or stalk kenozoid. Avicularia and ovicells absent.

Phase 2. Subcolony arising from long stalk of thinly calcified kenozoids derived from chambered pores at margins of phase 1 or phase 3 subcolonies. Stalk kenozoids in apposed pairs or triads, and bud elongated autozooids by the second to fifth astogenetic generation, followed by bifurcation of zooid rows to form bilaminar flustrine frond (Fig. 18b). Fronds 6–8 rows wide, increasing to 10–12 before simple bifurcation. Largest subcolonies extend for >90 astogenetic generations, bifurcate 4 times, and include over 2000 zooids. Marginal zooids elongated, but not kenozoids. Vertical walls of opposing laminae do not correspond, and simple septular pores communicate through basal walls. Zooids also have 1 distal, and 1 or 2 lateral multiporous septular pores. Autozooids very thinly calcified, with no gymnocyst or cryptocyst; frontal membrane continuous with simple, terminal crescentic operculum. Oral spines paired, terminal, arising from lateral walls, wide at base; short and frontally directed in autozooids; massive, swollen and curved over operculum in brooding zooids. Ovicells may be developed on all zooids except marginal zooids; large, prominent, hyperstomial and closed by operculum. Frontally ovicells slightly flattened, with median suture and paired, crescentic entooecial areas (Figs 30, 31). Number of tentacles 12–14 (Lt 0.75 mm, Lt sheath 0.20

mm). Avicularia scattered, usually proximal to, or at a bifurcation of zooid rows. Gymnoecyst thinly calcified, elongated, shorter in those avicularia at bifurcations; opesia uncalcified, rostrum raised and thickly calcified distally. Mandible subspatulate, hinged on paired condyles, directed distally (Fig. 3). Rhizoids arising from multiporous septular pores in walls of stalk kenozoids, or from autozooids at proximal end of fronds.

Phase 3. Subcolony bilaminar, forming subrectangular masses of 100–150 zooids, anchored by numerous rhizoids originating from enlarged marginal chambered pores. Subcolonies at tips of flustrine fronds, and proximal ends formed by 2 apposed series of 6–8 partially calcified zooids, alternating with next generation of zooids, which have frontal shield calcified at distal end only (Figs 25, 26). Following generation of 8–10 zooids elongated, with 16–18, often irregular costae, and prominent suboral bar. Subsequent 4 or 5 astogenetic generations have zooids with increasingly shorter and rounder costal shields, less prominent suboral bar, and smaller, semi-eircular calcified orifice. Pelmatidia in 2 concentric series, raised as blunt tubereles. 3 oral spines, becoming very large, swollen and fused, occluding orifice completely and developing large, blister-like pelmatidia on frontal surface. Large chambered pores at margins give rise to stalk kenozoids or rhizoids (Fig. 27, 28). Avicularia infrequent, occurring in earlier astogenetic generations, morphology same as those occurring in flustrine fronds. Ovicells absent.

**Remarks.** The nomenclatural consequences of the identity of *Cribrilina tubulifera*, *Watersia militaris* and *Corbulipora oriparma* are considerable, and are summarized in the synonymy given above. Although *Acanthocella* was introduced by Canu and Bassler (1917) with the Recent, Australian, *Cribrilina tubulifera* Hincks as type species, it was apparently their intention to erect a genus to receive the Eocene, Gulf of Mexico species, *A. erinacea* (Canu and Bassler, 1917: 36, pl. 4 fig. 1; 1920: 309, pl. 43 figs 101–103). *Acanthocella erinacea* has a frontal shield like that of *A. tubulifera* but has elongated ovicells without entooecial areas. It resembles the Recent, amphiAtlantic *Cribrilina sigularis floridana* Smitt (1873), which was referred to *Reginella* by Cheetham and Sandberg (1964), Cook (1985: 125, pl. 9F) and Winston (1982: 134, fig. 59), and which does not develop ovicells. One further species of *Acanthocella*, *A. clypeata* Canu and Bassler (1928: 39, pl. 4 figs 9, 10, Fig. 5) from the

Gulf of Mexico, has complex oral spines which incorporate the suboral bar (Ristedt, 1979). No ovicells have been described. *Acanthocella erinacea*, *R. floridana* and *A. clypeata* are not known to occur in more than one phase and are excluded from *Corbulipora* here. *Acanthocella erinacea* has been made the type species of *Castanoporina*, a new subgenus of the Cretaceous genus *Castanopora* by Voigt (1993). He described a new species, together with one originally introduced by Larwood (1962) as *Castanopora voigtii*. *Castanoporina voigtii* was illustrated by Voigt (1993: 148, pls 7, 8, 9) having both colonies and zooids with a strong resemblance to those of erect, phase 2 *Corbulipora ornata*. However, the zooids each have paired, adventitious oral avicularia and the ovicells have no entooecial frontal areas.

*Watersia* Levinsen (1909: 99) was informally introduced in a key to genera of Bieellariidae. In addition, *Watersia militaris* was mentioned twice (pp. 94, 95), although with no indication of author or date. However, Levinsen seems to have thus indicated *Flustra militaris* Waters as type species, as no other taxon was assigned to the genus *Watersia*, which was not mentioned again. *Flustra militaris* was originally described by Waters (1887a) from Port Jackson, New South Wales. His figure shows three apparently verticillate rows of brooding zooids, with membranous frontals, stout, 'club-shaped' oral spines, and ovicells with a median suture and paired frontal areas. The colony was described as 'bilaminar' and Waters noted the similarities in appearance of the ovicells with those of '*Flustra episcopalis*' (= *Euthyroides*).

Some specimens (ZMC, BMNH), four of which have labels in Waters' hand, or are from his collection, and all of which are from Port Jackson, have been examined. All the subcolonies were dry and very shrunken laterally, none possessed the earliest astogenetic stages of the flustrine phase. None of the subcolonies had any avicularia, which are generally rare in flustrine subcolonies with ovicells. Waters (1887a) did not mention avicularia in his original description. The verticillate appearance of the ovicelled specimens illustrated by Waters (1887a) is explained by the considerable lateral shrinkage which occurs when flustrine colonies are dried. The ovicells are prominent, but the very thinly calcified proximal parts of the zooids almost disappear from view. The length of the zooids of the subcolonies from New South Wales is consistently greater than 1.0 mm; longer than the zooids of this phase in the specimens from Bass Strait.

The structure of the ovicells resembles that of species of *Figularia*, as well as *Euthyroides*, and the similarities have been discussed and illustrated by Gordon (1989, pls 2, 30). It is interesting that the species illustrated as *Figularia mernae* Gordon (1989: 15, pl. 2C, D) from New Zealand, occurs with an encrusting and a flustrine phase.

*Corbulipora oriparma* was described in detail by Wass (1973, 1975). He particularly noted the astogenetic and ontogenetic changes occurring in the small, bilaminar subcolonies. He described the increasingly early occlusion of the zooidal orifices with astogeny, and speculated on the apparent impossibility of any tentacle protrusion in these zooids. He also described the changes in zooid shape with astogeny and spinous processes arising from the pelmatidia.

Among the 94 specimens examined, 27 include the transitional stages between phases. The commonest transition is that from the bilaminar to the flustrine phase (15 examples), with the transition from the encrusting to the flustrine phase being less frequent (nine examples). The transition from the flustrine to the bilaminar phase occurs in only three examples (Fig. 24). The total number of phase 1 subcolonies is 27, the majority (18) occurring from *Tangaroa* stn 155. The small subcolonies all encrust minute shell fragments, and some have the ancestrula visible. Some have a few marginal rhizoids, and one has a flustrine phase growing from stalk kenozooids. Stalk kenozooids developing from enlarged pores also occur in subcolonies from *Kimbla* stns 99 and 100, and *Tangaroa* stn 164. The kenozooids originate from adjacent chambered pores and are closely apposed in pairs or triads; their walls become attached to each other by the first astogenetic generation, and communicate with one another through septular pores. Zooids of the following generations are just as elongated, but have traces of an operculum present, and may have been capable of feeding early in their ontogeny. Some of these zooids develop thin calcification over their frontal walls later in ontogeny, and these develop multiporous septular pores, which are the origins of rhizoids 10–20 mm long. The total number of flustrine subcolonies is 40 and the largest occur from SLOPE stn 22 and *Tangaroa* stn 164, comprising 90 astogenetic generations and bifurcating four times. Ovicells are frequent, and when they are present, avicularia are rare. The flustrine subcolonies from *Kimbla* stn 100 and the 'Endeavour' sample, which have bilaminar phase 3 subcolonies developing at the tips of their fronds, have numerous avicularia but few

or no ovicells. The 27 bilaminar phase 3 subcolonies have the largest number of rhizoids (Cook, 1979). The number of flustrine subcolonies arising from the bilaminar phases seems to be limited only by the number of marginal kenozooidal chambers which have not already produced rhizoids. One specimen from the *Endeavour* sample has approximately 120 zooids, spanning five astogenetic generations, with partially calcified proximal zooids and nearly 60 marginal rhizoids, 10 mm long. Only one stalk kenozooid is present. On the other hand, one subcolony from SLOPE stn 22 has 11 stalks and 20 rhizoids emanating from a group of 70 zooids. If all these stalks developed into large, flustrine subcolonies, they would have the potential to produce more than 20,000 brooding zooids with ovicells. Some of the zooids from bilaminar subcolonies from *Kimbla* stns 99 and 100 have their interiors filled with orange tissue. Their orifices are completely occluded by the development and fusion of the oral spines. The tissue is reminiscent of that which fills the 'closed' zooids of some species of the genus *Conopeum* (Cook, 1985: 87), which can apparently function as hibernacula. It is inferred that if the closure of orifices is correlated with a non-feeding role for bilaminar subcolonies, the tissue-filled, closed zooids of *Corbulipora* may function as similar storage areas.

#### Notes on multiphased growth

Cloning by accidental fragmentation and subsequent isolation has been discussed for several colonial marine animals including Bryozoa by Jackson (1983). Cloning by specific series of astogenetic changes leading to the production of isolated subcolonies is known in the free-living, lunulitiform species of Cupuladriidae, particularly in the genus *Discoporella* (Cook, 1985; Winston, 1988). These species are components of sand fauna assemblages, and similar environments are associated with records of *Corbulipora tubulifera*, particularly those from the *Endeavour* sample (see above). Flustrine and bilaminar subcolonies were attached by their rhizoids to very large colonies of Catenicellidae and flustrine colonies of *Spiralaria*. These in turn were anchored to coelenterate colonies, and the entire mass was covered and intertwined with worm-tubes, sponges and smaller encrusting and creeping bryozoan colonies. Quantities of shell fragments and foraminiferans, together with sand grains were also present. This sample was from a locality and depth close to that from which another sample from Gabo Island originated,

which was analysed by Cook (1979). This comprised a similar assemblage of animals and colony forms, including subcolonies of bilaminar *C. tubulifera*. Both assemblages probably formed a mat on the surface of the bottom sediments. The minute shell fragments encrusted by the ancestrulae phase of *C. tubulifera* suggests that these subcolonies may have lived both on the surface and within the upper layers of the sediments. Interstitial colonies living on shell fragments were described by Winston and Håkansson (1986), and included several cribrimorph species. Although the records of *C. tubulifera* are from much deeper, and quieter waters, most from more than 50 m, and many from more than 100 m depth, an interstitial life would still be possible. The rhizoids which sometimes emanate from the growing margins of encrusting subcolonies would also help to anchor the large, erect, flustrine subcolonies as they grew, and before their own proximal rhizoids were developed later in ontogeny.

Bock and Cook (1994) have already speculated briefly on the roles of the different phases of *C. tubulifera* in establishing, extending and maintaining the colony asexually and sexually (Fig. 32). It is possible to infer similar roles among different phases of the two fossil species, *C. ornata* and *C. suggestens*. The encrusting subcolonies of both species are small; they inhabit a similar size of shell fragment substratum as those inhabited by *C. tubulifera*, and may well have lived in similar interstitial and semi-interstitial conditions. The erect, ovicellate phase of *C. ornata* is much more heavily calcified than the equivalent, flustrine phase of *C. tubulifera*, but would extend the colony and aid dispersal of larvae in the same way. Although there are numerous specimens of the small, bilaminar subcolonies of *C. suggestens* in the material examined, very few possess ovicells, and these occur only singly, near the proximal margins of the subcolonies on zooids with no costal frontal shield (Figs 28, 29). It seems reasonable to infer that, if the 'missing' cellularine or flustrine phase of *C. suggestens* existed, it too would have borne the majority of the ovicells. This inference is strengthened by the close similarity between the bilaminar phases of *C. tubulifera* and *C. suggestens*. Subcolonies of both species develop large chambered pores and kenozooids at the margins which are known to produce both stalk kenozooids and rhizoids in the Recent species. It has been inferred that the bilaminar phase is anchored by its rhizoids. After fracture of the delicate flustrine subcolonies it is isolated from the encrusting phase but stabilizes

and maintains the extended colony, also producing more flustrine phases and increasing the area occupied by the clone even further. To a certain extent this stabilizing role may be enhanced by the non-feeding nature of many zooids of the bilaminar phase and it is interesting that, although quite different in origin and subcolony structure, the kenozooidal third phase of *C. ornata* may have had a similar function. The kenozooidal masses also have large chambered pores etc., at the surface which may have given rise to rhizoids. Although much more robust than the erect phase of *C. tubulifera*, the quadriserial subcolonies of *C. ornata* may have also been susceptible to fracture, especially if they had originated from stalk kenozooids.

#### Notes on some other records of *Watersia*

*Watersia militaris* has not been fully described since its introduction and the genus *Watersia* has rarely been mentioned. Mawatari (1956) referred to '*Watersia kishakaensis*'. The synonymy included two previously described taxa, *Flustra simplex kishakaensis* Okada, 1918 and *Euthyroides simplex* Okada, 1921. These species are quite distinct from one another, although both have flustrine colonies and hyperstomial ovicells. *Watersia kishakaensis* has large ovicells with paired frontal entooecial areas, and small, interzooidal avicularia with rounded mandibles, orientated distally. *Euthyroides simplex* has much smaller ovicells and no avicularia. Dr Shunsuke Mawatari has kindly lent us some preparations of *W. kishakaensis*, together with some manuscript notes on species, made by his father, Dr Shizuo Mawatari. These confirm the separate identity of the two species, and the details of Mawatari's (1956: 121, fig. 5a) description. The ancestrula and early astogeny of neither *W. kishakaensis* nor *W. simplex* have been observed and described. Both species bear several resemblances to some Antarctic forms assigned to *Klugeflustra* by Moyano (1972), who introduced the genus for two flustrine species which had large, hyperstomial ovicells with paired, entooecial frontal areas. Both the type species, *Flustra vanhoeffeni* Kluge (1914), and *Flustra drygalskii* Kluge (1914), have colonies with broad bilaminar fronds, possess interzooidal avicularia, develop numerous rhizoids, and have recently been described from the Antarctic by Rosso (1994) and by Hayward (1995). Gordon (1985) regarded *Klugeflustra* as a junior synonym of *Watersia*, and although much more robust, both the Antarctic species resemble the *Watersia*-phase of *C.*

*tubulifera* in their colony form, thinly calcified zooids, spathulate avicularia and large ovicells. However, Ristedt (1991: 378, pl. 2 fig. 1) has described the early astogeny of *K. vanhoeffeni* in a specimen from the Weddell Sea ( $76^{\circ}55.2'S$ ,  $40^{\circ}58.9'W$ , 216–264 m). The ancestrula is very large (Lan 1.0 mm), encrusting and membraniporine, with no marginal or oral spines, gymnoecyst or cryptocyst. The encrusting base of the colony consists of approximately 50 similar autozooids. A specimen of *K. vanhoeffeni* from the South Shetland Islands (*Discovery* stn 1872, near Clarence and Elephant Islands,  $63^{\circ}29.6'S$ ,  $54^{\circ}03.1'W$ , 247 m, 12 Nov 1936), has been examined. The robust fronds are 45 mm in length, the zooids large, very thinly calcified, with no cryptocyst and two to three large, multiporous lateral septular pores. The avicularia are large, spathulate, and occur proximally to each bifurcation of zooid rows. The avicularia are raised distally and the descending part of the substral chamber is more heavily calcified than the rest, and appears white in contrast to the brown cuticle of surrounding walls. The proximal opercula are large and the mandible is hinged on a bar. Ovicells occur in identical bands on both sides of the fronds, five to seven astogenetic generations deep, and at intervals of about five generations apart. Ovicells are very large, are closed by the partially open operculum, and have a pair of long, irregular frontal entooecial areas flanking a central suture. These may be subdivided into four foramina in some cases.

In spite of the close similarities between *K. vanhoeffeni* and the *Watersia*-phase of *C. tubulifera*, the complete lack of a cribromorph phase in early astogeny, suggests that the genus *Klugeflustra* should be maintained for the Japanese and Antarctic species described above.

One further Antarctic flustrine genus, *Neoflustra* Lopez Gappa (1982), is also known to have hyperstomial ovicells, but these do not have frontal entooecial areas. The avicularia are numerous but adventitious and occur on a distinct proximal zooidal gymnoecyst. It is interesting that although the autozooids of the type species, *N. dimorpha*, have no spines, the brooding zooids bear several pairs of flattened, overarched, marginal spines, the distal pair being enlarged like those on the brooding zooids of the *Watersia*-phase of *C. tubulifera*. *Klugeflustra kishakaensis*, *K. simplex*, *K. vanhoeffeni* and *K. drygalskii*, together with *Neoflustra*, form a distinctive subgroup, at present classified within the Flustridae. Their ovicell structure is so unlike that found in all other members of the family, however, that it

seems almost certain that a new family grouping may be eventually required to accommodate them. However, little more can be inferred without much more information about the early astogenetic stages of colonies. The relationship of these genera with *Corbulipora*, and the Cribriomorpha in general, is even more obscure and cannot be evaluated until more is known about the occurrence of multiphase growth within the Bryozoa.

The records of *Watersia* sp. (Gordon 1985) and of *Watersia militaris* from New Zealand given by Livingstone (1929) and by Gordon (1986), are not referable to the genera and species discussed here, but belong to the anascan family Calloporidae (Cook and Bock, 2000).

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**Appendix.** Details of Tertiary localities in south-eastern Australia

Bairnsdale (Skinner's): Mitchell R. bank, about 12 km W of Bairnsdale, Vic.  $37^{\circ}47.9'S$ ,  $147^{\circ}29.5'E$ . Miocene.

Balcombe Bay: also known as Fossil Beach, Mornington, Mount Martha and possibly 'Schnapper Point' (MacGillivray); on coast of Port Phillip Bay, about 3 km S of Mornington, Vic.  $38^{\circ}14.5'S$ ,  $145^{\circ}01.7'E$ . Fyansford Clay. Balcombian; Middle Miocene, (Langhian).

Bird Rock: Coastal section, about 3 km W of Torquay, Vic.  $38^{\circ}21.4'S$ ,  $144^{\circ}17.8'E$ . Jan Juc Formation. Janjukian; Late Oligocene, (Chattian). Also known as Spring Creek.

Campbells Point: On Lake Connewarre, 12.5 km SE of Geelong, Vic.  $38^{\circ}13.7'S$ ,  $144^{\circ}26.7'E$ . Middle Miocene.

Cape Otway: also Point Flinders. Locality AW1. Coastal section 2 km NW of Cape Otway, Vic.  $38^{\circ}51.1'S$ ,  $143^{\circ}29.5'E$ . Glen Aire Clay. Early Oligocene (Rupelian/Latdorian).

Cooriemungle area: road cuttings about 18 km N of Princetown.  $38^{\circ}32.4'S$ ,  $143^{\circ}08.1'E$ . Gellibrand Marl. Balcombian.

Curdies Creek: this is the locality name applied to the bryozoans described by Waters (1881). The original paper mentions 'Yarra Yarra', which is the river on which Melbourne is located, and from which no bryozoan fossil localities have been

recorded. Later publications (e.g. MacGillivray, 1895) have used the locality Curdies Creek for this collection. The coastal section at the mouth of the Curdies R. exposes Late Miocene limestone with a sparse bryozoan fauna. Inland sections are generally in limestone but some of the muddy sediments of the Gellibrand Marl are exposed near Timboon. However, it is believed that the sample is more likely to have come from coastal sections, which were much more accessible at that time. If the sample was obtained from the coastal exposure, it almost certainly was close to the locality listed as 'Princetown' below.

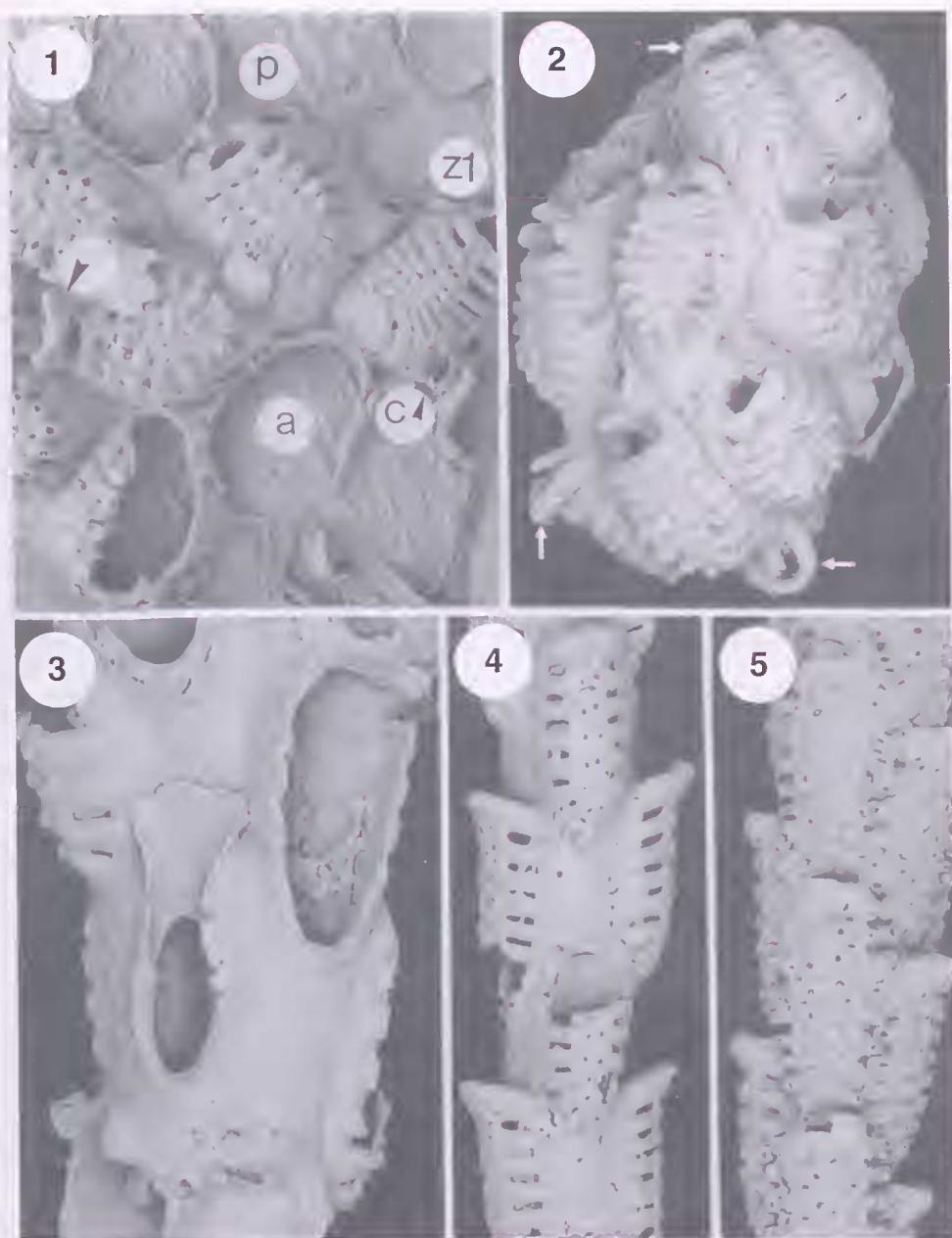
Grices Creek: also known as Gunyong Creek; on coast of Port Phillip Bay, about 8 km N of Mornington, Vic.  $38^{\circ}11.9'S$ ,  $145^{\circ}03.9'E$ . Fyansford Clay. Balcombian (some material may be Bairnsdalian); Middle Miocene, (Langhian).

Mount Schanck: limestone quarry about 1 km W of Mount Schanck, about 15 km S of Mount Gambier, SA.  $37^{\circ}57'S$ ,  $140^{\circ}43.2'E$ . Gambier Limestone. Longfordian; Early Miocene.

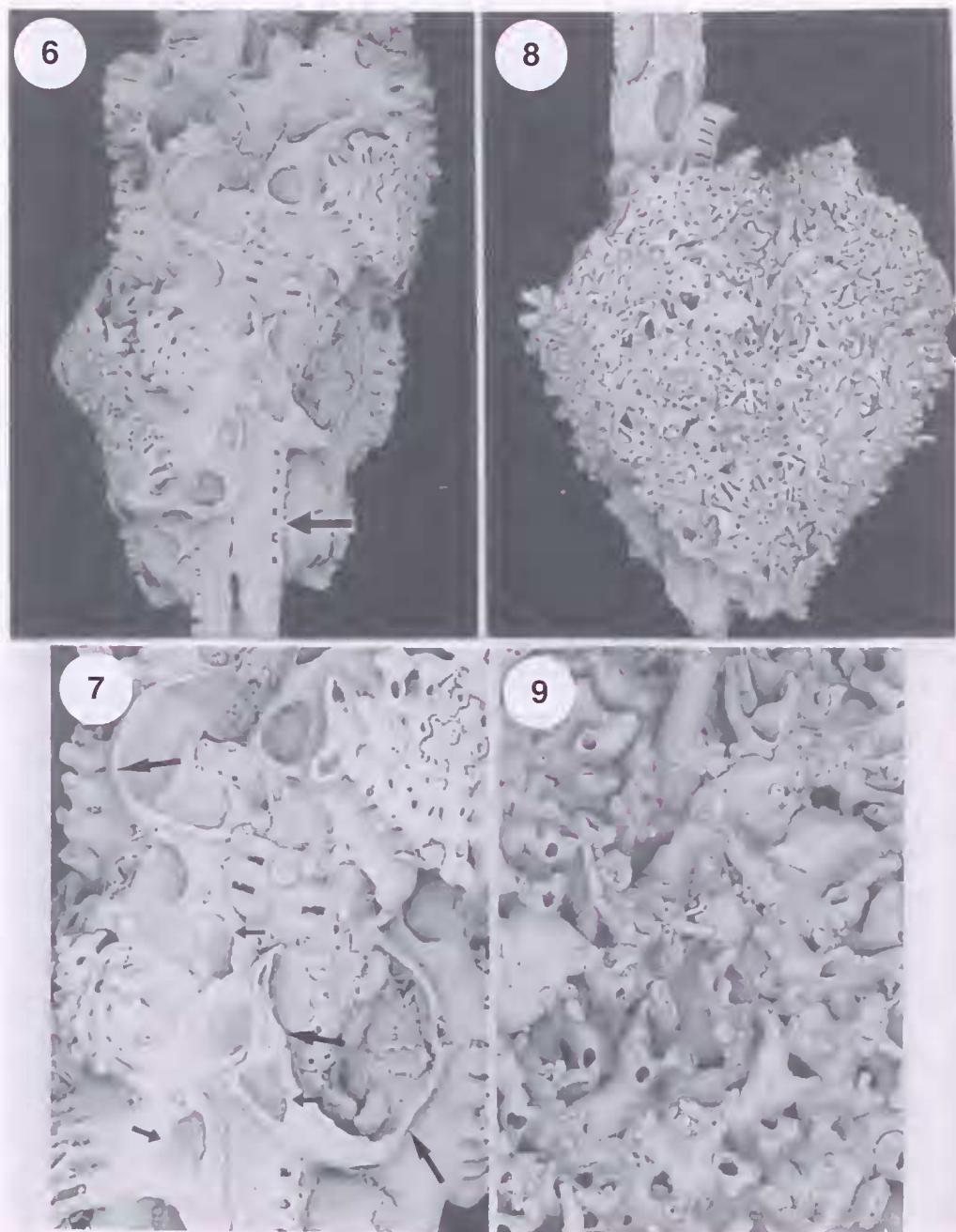
Muddy Creek: Clifton Bank, Muddy Creek, 8 km W of Hamilton, Vic.  $37^{\circ}44.6'S$ ,  $141^{\circ}56.4'E$ , Muddy Creek Marl (= Gellibrand Marl), Balcombian.

Narrawaturk Bore 2: at Peterborough, Vic.  $38^{\circ}36.3'S$ ,  $142^{\circ}52.3'E$ . Core 9, 522.1–526.4 m. Gellibrand Marl. Early Miocene (Longfordian).

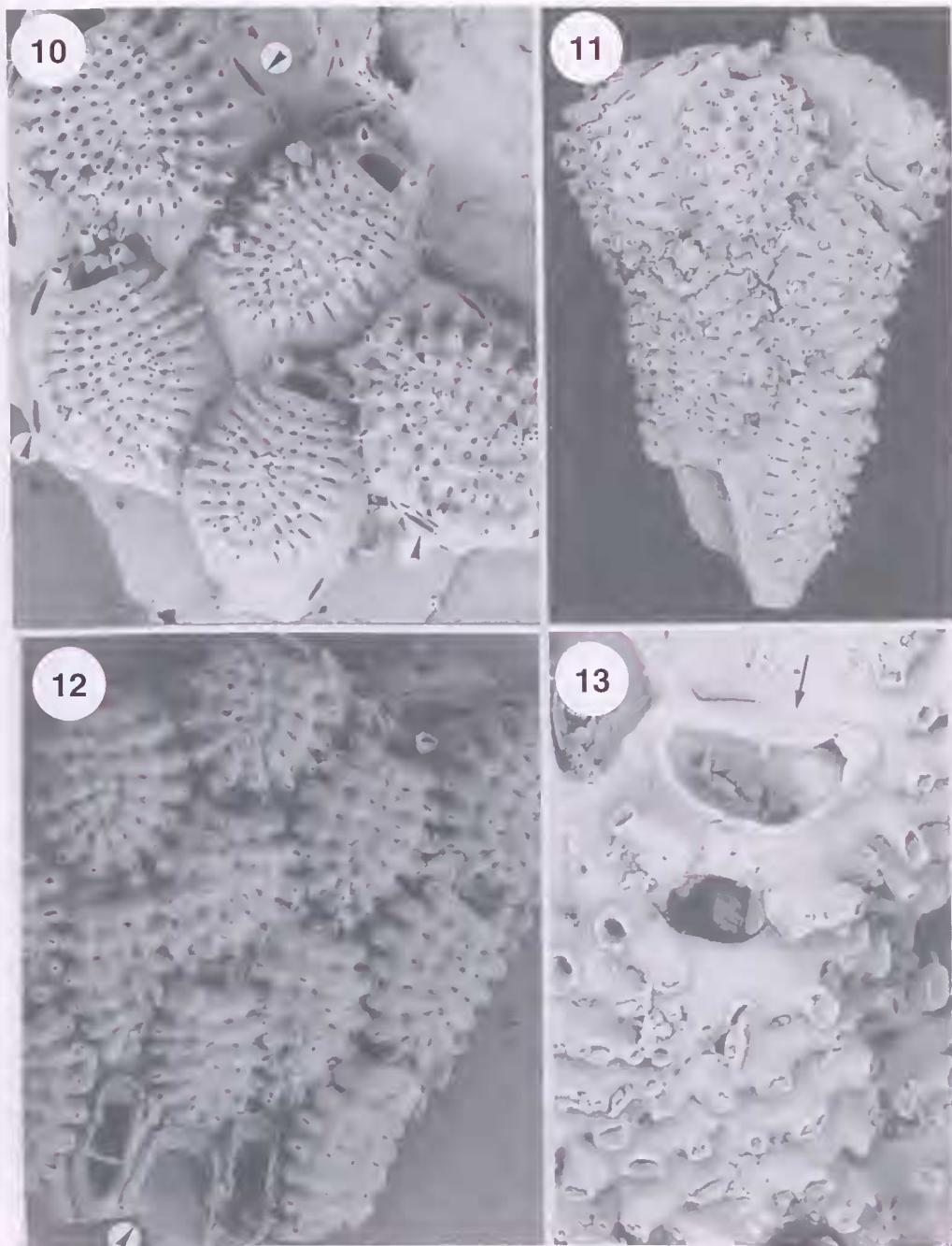
Princetown (*Gigantocypraea* locality): coastal section, about 2 km W of Princetown, Vic.  $38^{\circ}41.9'S$ ,  $143^{\circ}08.3'E$ , Gellibrand Marl. Balcombian.



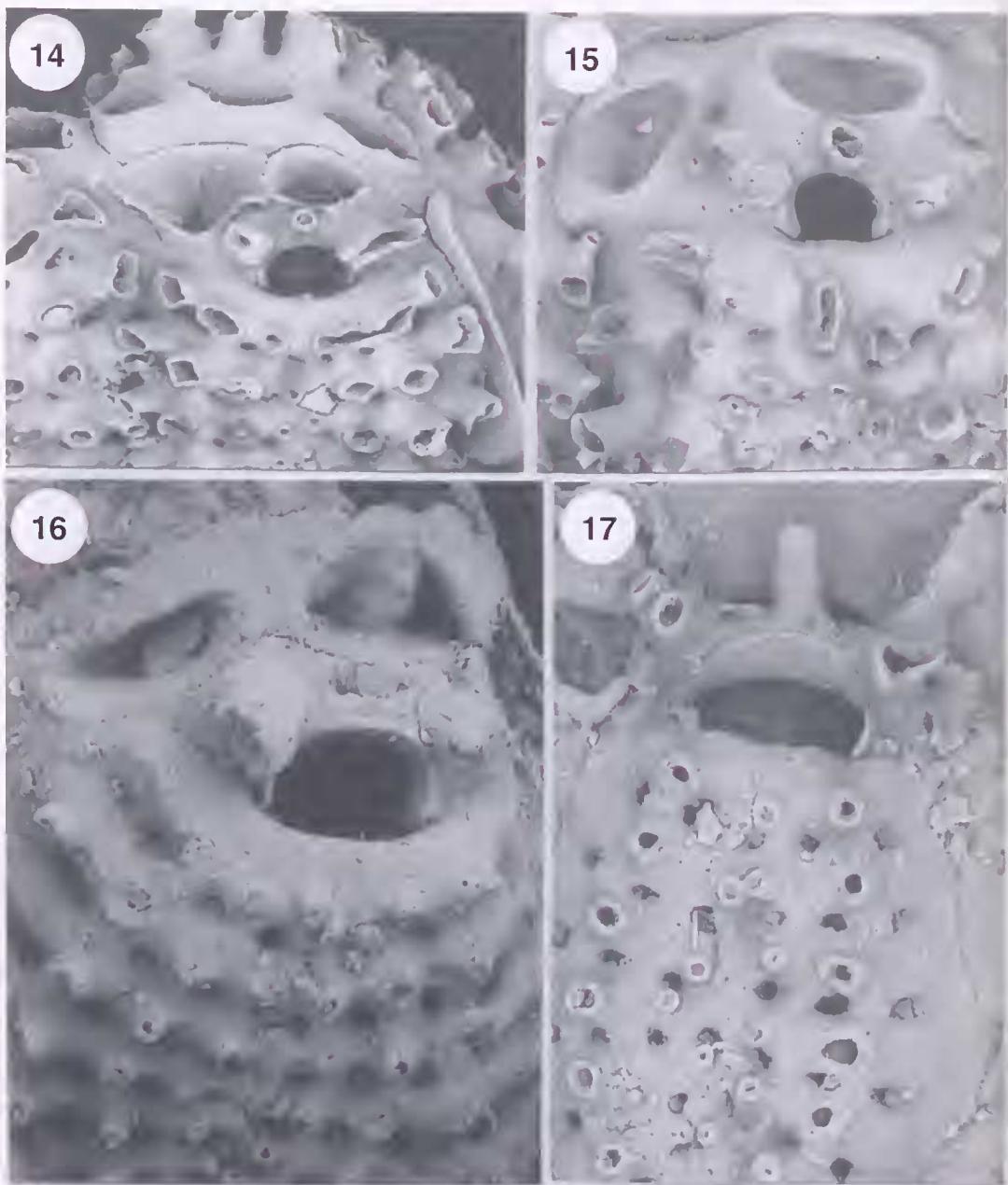
Figures 1–5. *Corbulipora ornata*. Figs 1–2, Mount Schanck, SA, encrusting, phase 1 subcolonies. Fig. 1, ancestrula (a) and primary triad of zooids. Note that the first distal zooid (z1) has costae with no lateral fusions; the second and third zooids have costae with lateral fusions and raised marginal spinous processes. Note pore chambers (p), potential frontal bud arising from raised chambered pore (c), and raised, medially fused oral spines on the third zooid (arrowed) ( $\times 70$ ). Fig. 2, encrusting, globular subcolony, showing raised, medially fused oral spines (arrowed) ( $\times 62$ ). Figs 3–5, Balcombe Bay, Vic., creet, phase 2 subcolonies. Fig. 3, zooids early in ontogeny with long gynoecyst and small, simple costate shield (incomplete or worn), and avicularium with distally expanded rostrum and paired condyles ( $\times 80$ ). Fig. 4, zooids later in ontogeny with median arca of frontal shield with pelmatidia ( $\times 50$ ). Fig. 5, zooids late in ontogeny with numerous, raised pelmatidia and prominent suboral bar ( $\times 42$ ).



Figures 6–9. *Corbulipora ornata*. Balcombe Bay, Vic., subcolonies of erect, phase 2 and kenozooidal, phase 3 zooids. Fig. 6, note central column of phase 2 zooids surrounded by frontally budded costate zooids and kenozooids (arrowed)  $\times 45$ . Fig. 7, enlargement of zooids, note marginal chambered pores (small arrows), and raised walls of partially calcified kenozooids (large arrows), all originating above the pelmatidia of underlying, phase 2 zooids ( $\times 70$ ). Figs 8–9, later astogenetic stages. Fig. 8, subcolony showing mass of spinous frontal shields of autozooids and kenozooids, the outlines of which are no longer visible. The central core of the original erect, phase 2 subcolony zooids is visible distally and proximally ( $\times 30$ ). Fig. 9, enlarged portion of the same subcolony ( $\times 100$ ).



Figures 10–13. *Corbulipora suggerens*. Fig. 10, Prineetown, Vie., encrusting, phase 1 subcolony, zooids showing spinous, eostate frontal shields; pore chambers (arrowed) ( $\times 50$ ). Fig. 11, Balcombe Bay, Vie., bilaminar, phase 3 subcolony arising from paired, proximal zooids ( $\times 70$ ). Fig. 12, Mount Schanck, SA, slightly wider, bilaminar, phase 3 subcolony, with paired proximal avicularia and zooid with uncalcified frontal (arrowed) ( $\times 64$ ). Fig. 13, Balecombe Bay, Vic., enlargement of zooid from distal part of subcolony in Fig. 11, showing large, frontally uncalcified, distal kenozoid arising from chambered pore (arrowed) ( $\times 160$ ).



Figures 14–17. *Corbulipora suggerens*. Figs 14–15, Balecombe Bay, Vic., zooids from distal margin of subcolony in Fig. 11, showing large kenozooids arising from distal chambered pores; note relatively small size of the calcified orifice. Fig. 14 ( $\times 120$ ). Fig. 15 ( $\times 150$ ). Compare both figures with the origin of stalk kenozooids of *C. tubulifera* illustrated in Fig. 20. Fig. 16, Princetown, Vie., single zooid from encrusting, phase I subcolony showing frontal shield and oral spines. Note large chambered pore surrounding distal oral spine, probably derived from a pore chamber, and relatively small size of calcified orifice. Compare with *C. tubulifera*, Fig. 17 ( $\times 210$ ). Figure 17. *Corbulipora tubulifera*. Tangaroa stn 155, Bass Strait, single zooid showing frontal shield and oral spines. Note relatively large size of calcified orifice ( $\times 200$ ).

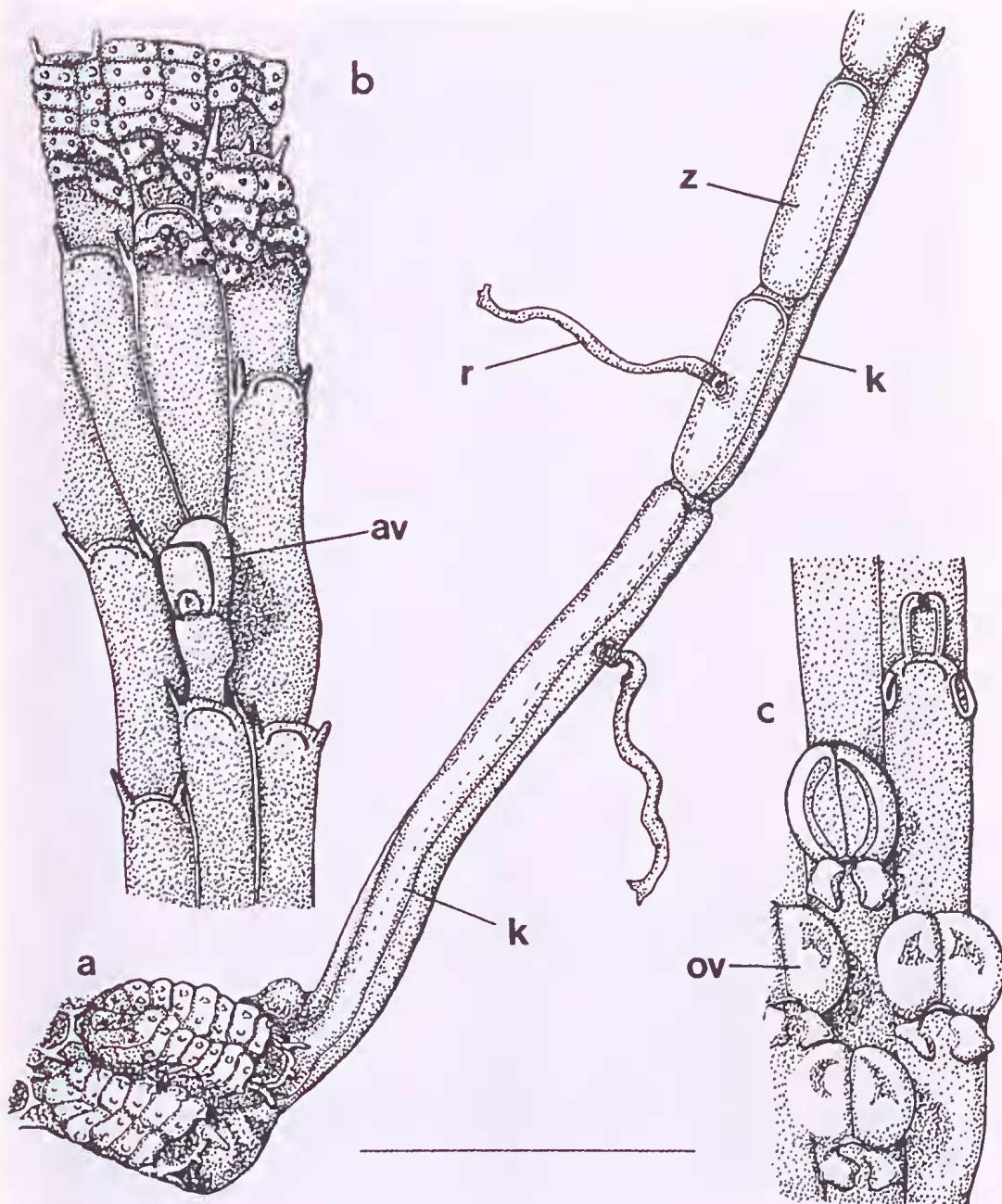
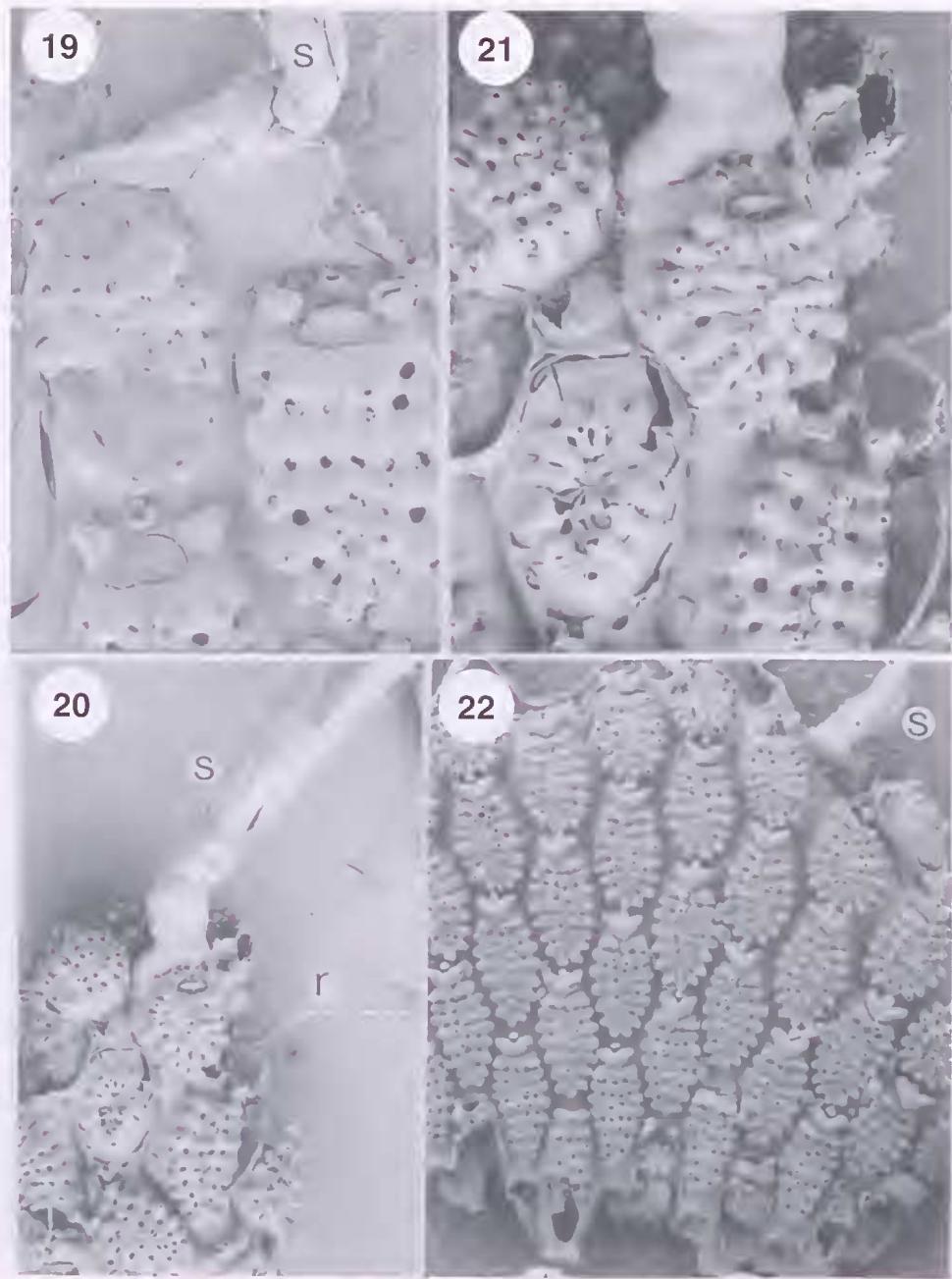
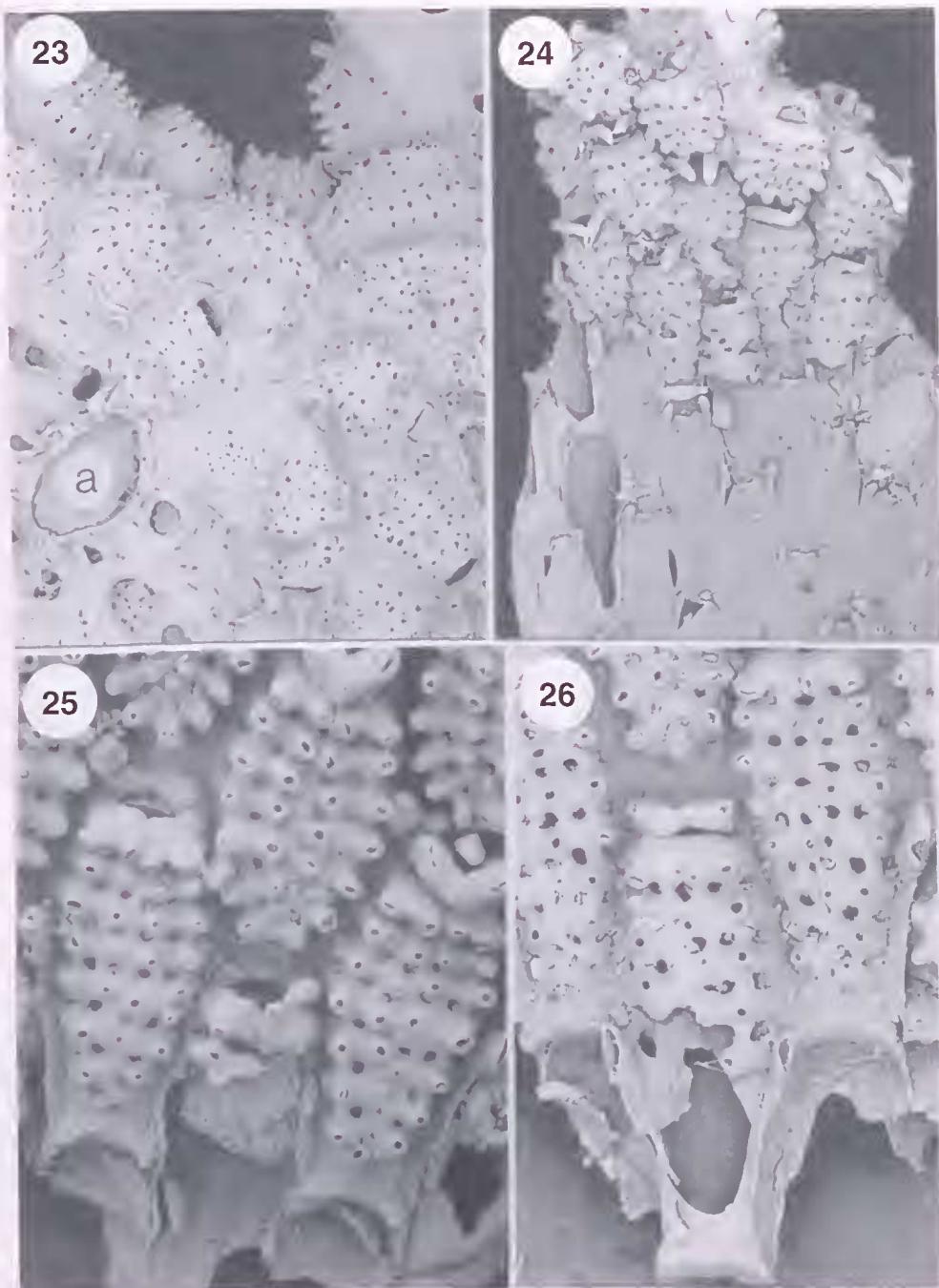


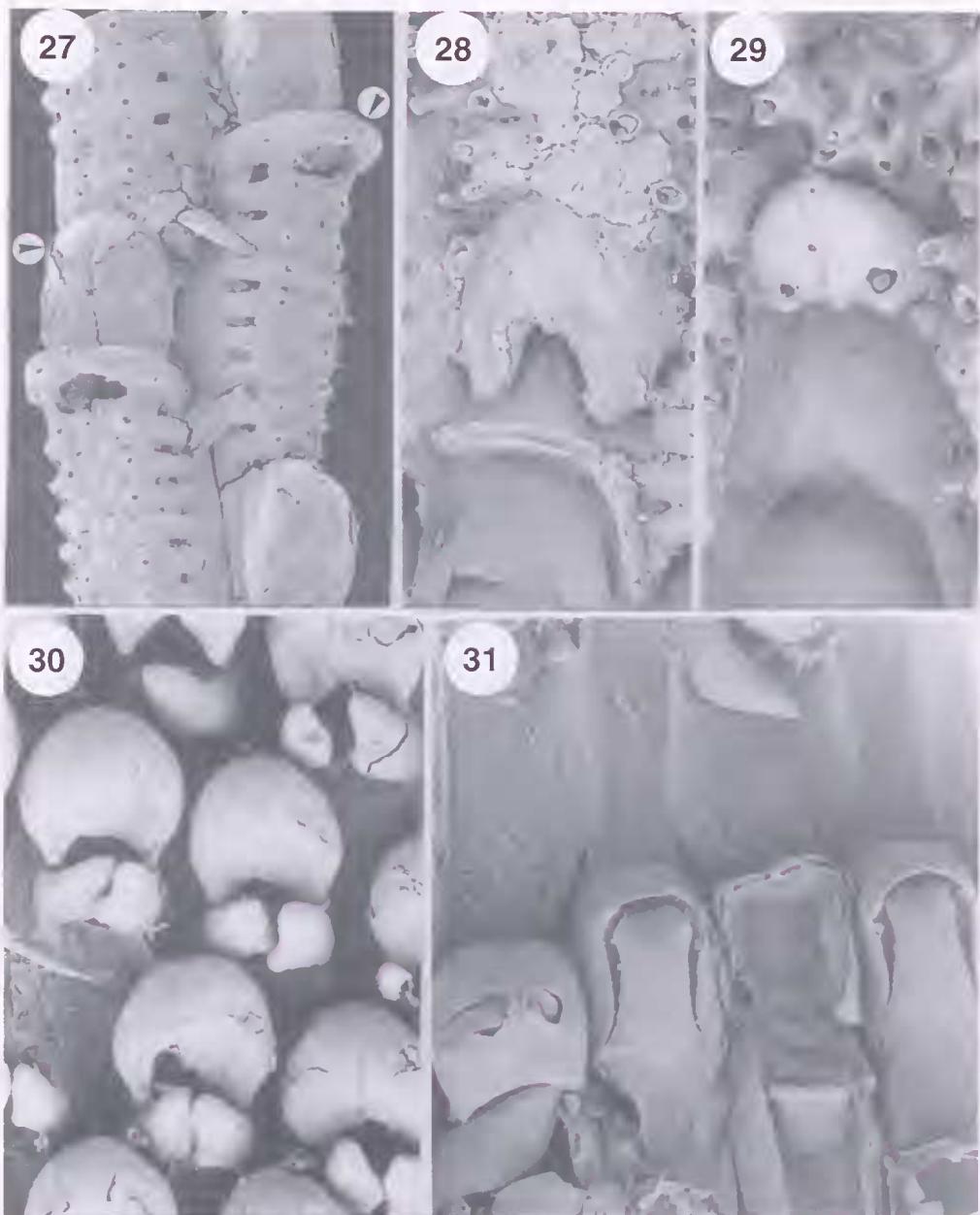
Figure 18. *Corbulipora tubulifera*, characteristics of phases. a. encrusting, phase 1 zooids with stalk kenozooids (k), arising from marginal chambered pores, developing rhizoids (r) and budding autozooids (z) at the base of an erect, flustrine phase 2 subcolony. b. tip of a frond of a flustrine, phase 2 subcolony, with an avicularium (av), and developing distal transitional zooids and bilaminar, phase 3 zooids with costate frontal shields (see also Fig. 24). c. zoids of flustrine, phase 2 subcolony with ovicells (ov) and large oral spines. Scale = 0.60 mm.



Figures 19–22. *Corbulipora tubulifera*. Bass Strait. Fig. 19, *Tangaroa* stn 155, encrusting, phase 1 autozooids with distal stalk kenozooid (s), arising from chambered pores; note autozooid frontal membranes and opercula ( $\times 80$ ). Figs 20–22, *Kimbla* stn 100. Fig. 20, small, bilaminar, phase 3 subcolony, with rhizoids (r) and a pair of large stalk kenozooids (s), see also Fig. 21 ( $\times 35$ ). Fig. 21, enlargement of zooids from Fig. 20, showing origin of stalk kenozooids from distal chambered pores; compare with Figs 14 and 15 ( $\times 80$ ). Fig. 22, bilaminar, phase 3 subcolony with distal rhizoids and a stalk kenozooid (s); proximal autozooids with partially calcified frontal shields (arrowed); see also Figs 25 and 26. Note progressive, distally directed closure of zooid orifices by fused oral spines ( $\times 28$ ).



Figures 23–26. *Corbulipora tubulifera*. Bass Strait. Fig. 23, Tangaroa stn 155, early astogeny of an encrusting, phase 1 subcolony, on an adeonid bryozoan; ancestrula (a) ( $\times 46$ ). Figs 24–26, Kimbla stn 100. Fig. 24, part of a flustrine, phase 2 frond, developing transitional distal zooids, and phase 3, calcified zooids at the tip ( $\times 31$ ); compare with Fig. 18b. Figs 25 and 26, zooids with uncalcified or partially calcified frontal shields from proximal zone of transition from phase 2 to phase 3 subcolony shown in Fig. 22. ( $\times 90$ ).



Figures 27–31. Ovicells in *Corbulipora*. Fig. 27, *Corbulipora ornata*, Balcombe Bay, Vic. Brooding zooids of erect, phase 2 subcolony, showing ovicells. Crescentic entoocial area (arrowed) and raised, medially fused oral spines (arrowed) ( $\times 75$ ). Figures 28 and 29, *Corbulipora suggereens*. Fig. 28, Balcombe Bay, Vic., brooding zoid with uncalcified frontal shield and ovicell with crescentic entoocial areas ( $\times 130$ ). Fig. 29, Princetown, Vic., brooding zoid with uncalcified frontal shield and ovicell with paired pores ( $\times 200$ ). Figures 30 and 31, *Corbulipora tuberculata*, Bass Strait, Tangaroa stn 164. Fig. 30, brooding zooids from flustrine, phase 2 subcolony, showing uncalcified frontal membranes, enlarged oral spines and ovicells with crescentic entoocial areas ( $\times 80$ ). Fig. 31, part of a flustrine, phase 2 subcolony, showing uncalcified frontal membranes, one ovicell and two avicularia ( $\times 100$ ).

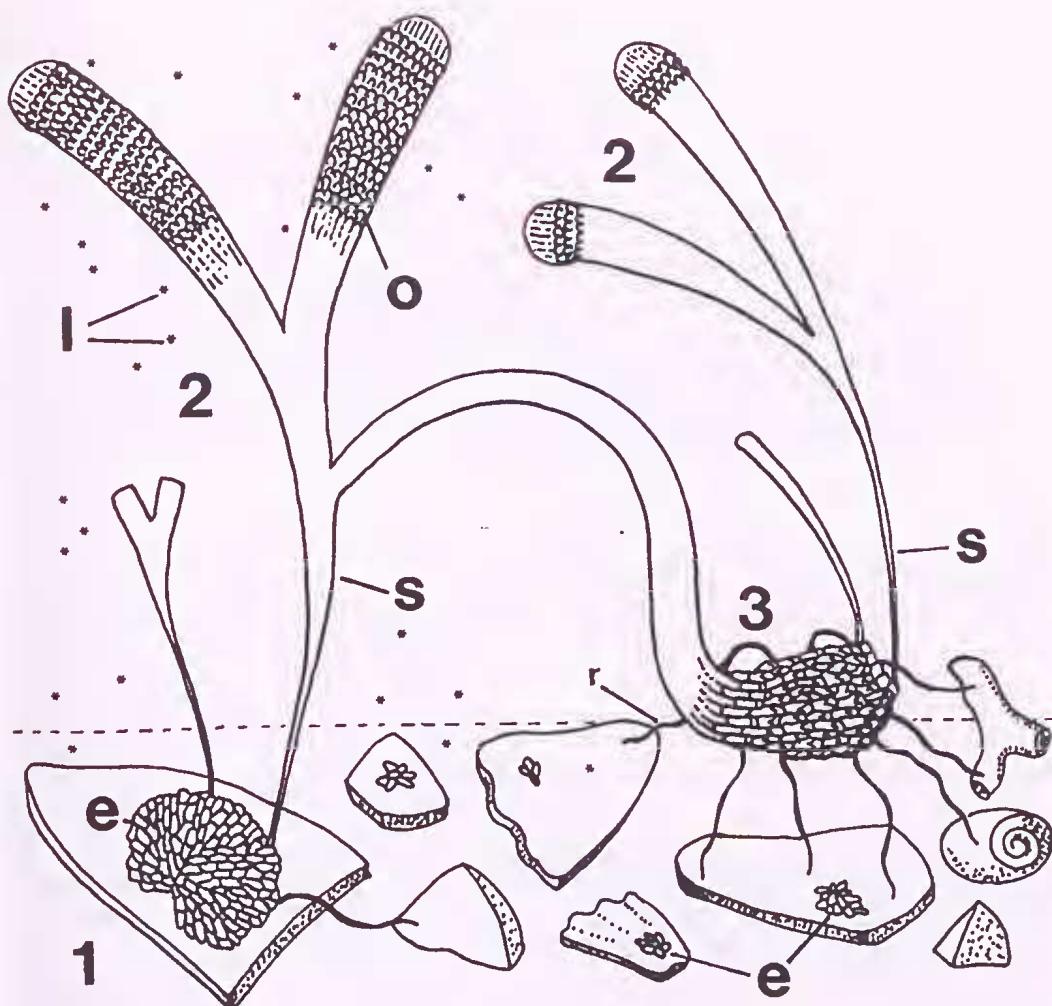


Figure 32. Diagram of inferred roles of different phases in *Corbulipora tubulifera*. 1. encrusting phase (e) establishes subcolony on shell fragment which becomes anchored by rhizoids in and on the surface layers of sediment. 2. erect flustrine phase arises from stalk kenozoids (s), budded from marginal chambered pores of phase 1 zooids. Flustrine phase produces brooding zooids with ovicells (o), which brood embryos of motile larvae (l), which disperse and settle on shell fragments, metamorphosing and producing ancestrulae, which bud new, phase 1 subcolonies (e). 3. bilaminar phase originates from the tips of fronds of the flustrine phase, and becomes anchored on surface of sediment by rhizoids (r). These subcolonies maintain the area occupied by the flustrine phase 2 subcolonies, even if they become isolated. Phase 3 subcolonies then bud further phase 2, flustrine subcolonies from marginal stalk kenozoids (s), and repeat the sexually reproductive phase. Not to scale.